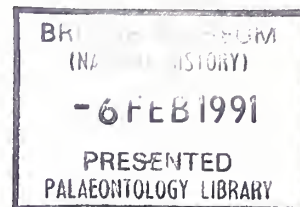


# The Carboniferous pteridosperm frond *Neuropteris heterophylla* (Brongniart) Sternberg



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**SYNOPSIS.** New evidence on the frond architecture of *Neuropteris heterophylla* (Brongniart) Sternberg is presented, based on well-preserved adpressions from Clay Cross, Derbyshire. Their cuticles provide the first reported evidence of epidermal structure for this species, including remains of trichomes apparently with *in situ* exudate. The new evidence indicates that this species is more closely related to *Neuropteris ovata* Hoffmann and *Neuropteris flexuosa* Sternberg, rather than to *Laveineopteris loshii* (Brongniart) Cleal *et al.* and *Laveineopteris tenuifolia* (Sternberg) Cleal *et al.*, as argued by some previous authors.

## INTRODUCTION

*Neuropteris* (Brongniart) Sternberg is one of the most widely reported macrofossil form-genera from the Westphalian of Europe and North America. It represents foliage of an extinct group of gymnospermous plants known as the Trigonocarpaceae Meyen 1987 (Medullosales *auctt.*), which probably grew on levee banks and other raised areas within the equatorial delta plains of the time (Zodrow & Cleal 1988). Recently, our understanding of the form-genus has significantly improved, particularly as a result of frond architecture and cuticle studies (Barthel 1961, 1962, 1976; Reichel & Barthel 1964; Laveine 1966a, 1966b, 1967, 1987; Laveine & Brousmiche 1982; Zodrow & Cleal 1988; Cleal & Zodrow 1989), and it has become evident that the form-genus is far from homogeneous. As a result, some species have been transferred to other form-genera (e.g. *Paripteris* Gothan, *Neurallethopteris* Cremer *ex* Laveine – see Laveine, 1967) but, until recently,

most have been retained in *Neuropteris*. This was partly because the frond of the type-species (*N. heterophylla* (Brongniart) Sternberg, 1825) had not been fully reconstructed, nor was anything known of its epidermal structure. Consequently, it was not possible to say which of the groups recognizable on, say, epidermal structure represented real *Neuropteris*, and which needed to be transferred to other form-genera.

The type species was first published as *Filicites* (*Neuropteris*) *heterophyllus* by Brongniart (1822), and was later changed to *Neuropteris heterophylla* (Brongniart) by Sternberg (1825). (Few subsequent authors have recognized the validity of Sternberg's initial publication of this combination, which is often attributed incorrectly to Brongniart (1828) – e.g. Crookall 1959, Laveine 1967). The small holotype was illustrated diagrammatically only (Brongniart 1822: pl. 2, figs 6a, b) and is now reported lost (Laveine 1967). Many authors have regarded it as conspecific with *Laveineopteris loshii* (Brongniart) Cleal *et al.* 1990 (e.g. Stockmans 1933, Havlena 1953, Crookall 1959), a common species distributed widely

through the Westphalian A–C of Europe. Laveine (1967) has argued that this is unlikely, however, basing his contention mainly on a rather larger specimen of *N. heterophylla* figured by Brongniart (1831: pl. 71). This latter specimen is clearly quite different from *Laveineopteris loshii*, and hence many traditional conceptions about *N. heterophylla* (and consequently of the form-genus *Neuropteris* itself) would appear to be ill-founded. *N. heterophylla* as interpreted by Laveine (1967) is in fact an uncommon species; his synonymy refers to only ten undoubted specimens illustrated in the literature, and he figured another three.

The present paper documents some large and excellently preserved specimens in the palaeontological collections of the British Museum (Natural History), from which we have been able to provide a detailed reconstruction of the frond. Some of these specimens also yielded cuticles. The only previous record of *N. heterophylla* cuticles is by Wills (1914), based on specimens from North Wales. As we will argue later, however, Wills' material is almost certainly misidentified, and our specimens provide the first unequivocal evidence of the epidermal structure of this species. The results presented here have important consequences for the generic classification of neuropterid foliage, and have been the basis of the revised classification published by Cleal *et al.* (1990).

## MATERIALS

This study is based largely on eight hand-specimens stored in the Department of Palaeontology, British Museum (Natural History) (Accession Numbers V.1797, V.1867, V.1868, V.1871, V.1872, V.2727, V.63152, V.63153). They are all labelled as originating from the 'Coal Measures, Clay Cross, Derbyshire'. No further stratigraphical details are given, but they probably came from the Westphalian B. Cuticles were prepared from four of these specimens: V.1867, V.1868, V.2727 and V.63152.

## METHODS

The hand-specimens were photographed using crossed-polar filters. Because of limited page size, we cannot reproduce photographically all the specimens at the same scale; tracings from the photographs are therefore reproduced here at a uniform scale of  $\times \frac{1}{3}$  (Figs 26–28).

Cuticles were prepared using the method outlined by Barthel (1962). Pieces of fossil were removed from the hand-specimens with a small chisel, and then placed in 40% hydrofluoric acid to remove the rock matrix (pre-treatment with hydrochloric acid was found to be unnecessary). The carbonaceous phytolite (sensu Krystofovich 1944) were next oxidized in Schultze's Solution for 1–2 hours, and then treated with a 5% solution of ammonium hydroxide to remove the soluble oxidation products. The resulting cuticles were washed thoroughly in distilled water.

Most of the cuticles were mounted in glycerine jelly containing safranin dye. They were examined with a Leitz Ortholux II microscope, using differential interference phase contrast (Normarski contrast) at high magnifications. In addition,

some cuticles were mounted on stubs, thinly coated with gold, and examined at 15 kV with an Hitachi S-800 field emission scanning electron microscope.

## DESCRIPTIONS

### Frond architecture

In their gross morphology, the specimens dealt with in this paper basically fall into two groups: wide tripinnate pinnae with broad primary rachis; and distally tapered, tripinnate pinnae. These are interpreted as proximal and distal fragments of the frond, respectively, and are most conveniently described separately.

*Proximal frond fragments* (Figs 1, 2, 26 and 27a). The most proximal part of the frond preserved in these specimens (Fig. 1) shows a primary rachis, 2.5 cm wide, that extends for 1.5 cm before branching dichotomously. The resulting branches lie at 90° to each other near the fork, but then gradually curve inwards towards each other. This curvature is achieved, at least in part, by a series of kinks occurring at about the points of attachment of each secondary pinna on the outward-facing side of the primary rachis (Fig. 2). The primary rachis above the dichotomy are 1.2–1.5 cm wide, tapering to c. 0.5 cm wide in the most distal part of the specimens (Figs 1, 2).

The overall shape of the two primary pinnae produced by the dichotomous primary rachis is not shown in these specimens, but they appear to taper proximally, at least on their inward-facing side. Each primary pinna is markedly asymmetrical, although they are essentially symmetrical to each other about the long axis of the frond (Fig. 1). On the outward-facing side of the primary rachis branches, robust secondary pinnae with rachis 0.5–0.6 cm wide are attached at 60°–70°, at intervals of 8–10 cm. Very little of these secondary pinnae is preserved, the longest fragment being only 15 cm long and clearly very incomplete, but they appear to be bipinnate (Fig. 1). Their shape cannot be determined from the fragments preserved. In between these large bipinnate secondary pinnae are much shorter (3–4 cm long) monopinnate intercalated pinnae spaced at 2–3 cm intervals (Fig. 2). They are tapered and terminated by a single rhomboidal apical pinnule.

On the inward-facing side of each primary rachis branch, secondary pinnae are inserted at intervals of 3–5 cm, usually at an angle of 70°–90°. They are 3 cm long and monopinnate near the base of the primary rachis branch (Fig. 1), becoming 30 cm long and bipinnate in the more distal parts (Fig. 2). Adjacent secondary pinnae overlap slightly in the middle of the frond. They appear tapered for much of their length, except in the longer ones which are parallel-sided in their proximal part, and are terminated by a single rhomboidal apical pinnule. There is little evidence of marked differentiation in development of the secondary pinnae, such as is seen on the outward-facing side of the primary rachis, but when they start to become bipinnate (some 20 cm from the base of the specimen), alternate secondary pinnae become shorter and less divided.

Another specimen with an apparently curved primary rachis is shown in Figs 3 and 27b. The primary rachis is c. 1.5 cm wide, tapering distally to 1.0 cm wide. Bipinnate

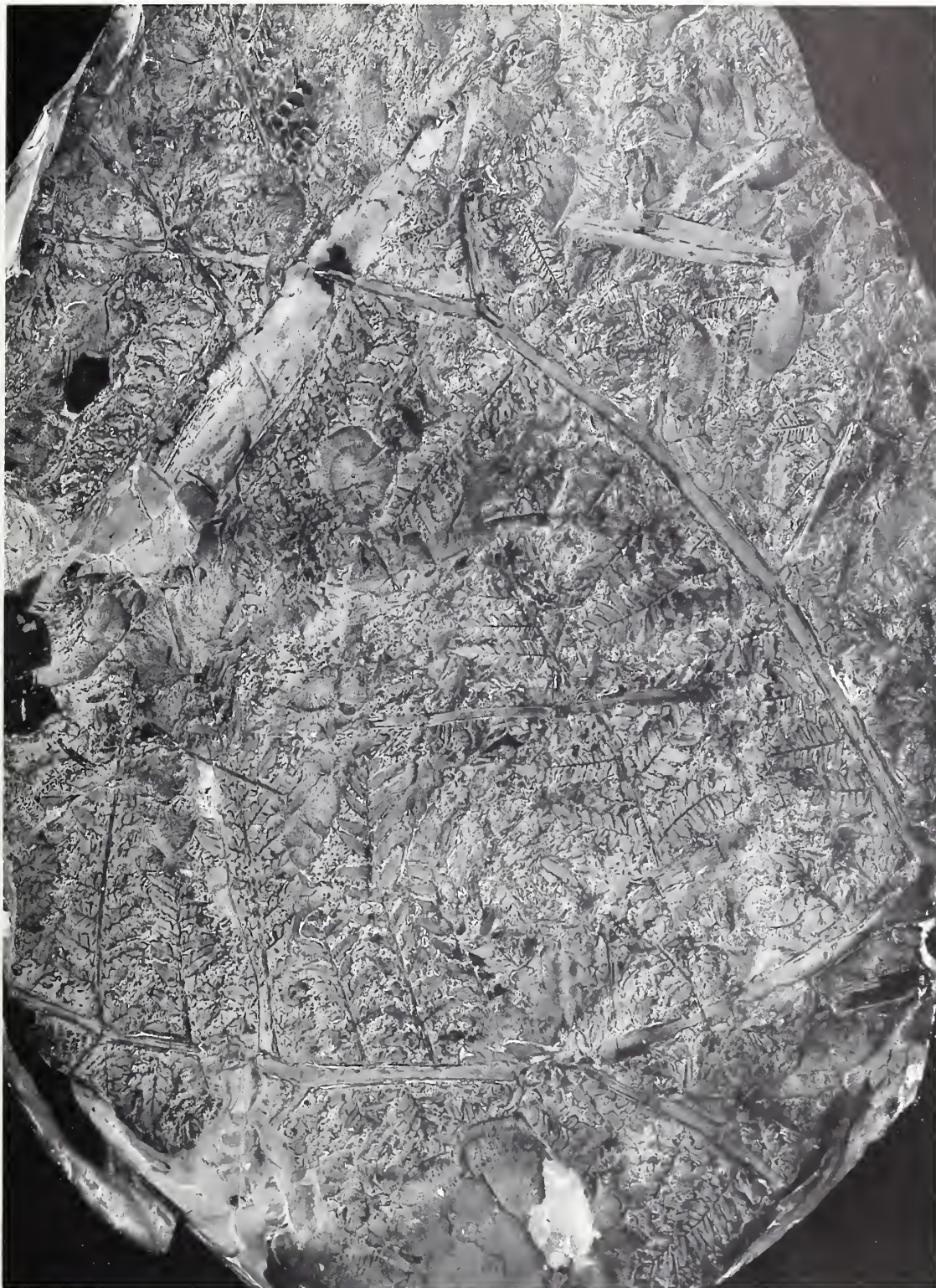


Fig. 1 *Neuropteris heterophylla*. Basal part of frond, showing dichotomy of primary rachis, photographed with crossed-polar filters. V.1797,  $\times \frac{1}{3}$ . See also Fig. 26.

secondary pinnae are attached at  $60^{\circ}$ – $70^{\circ}$  at c. 6 cm intervals on the right side of the specimen, but there is little evidence of secondary pinnae on the other side except for one short stump of secondary rachis. Short monopinnate pinnae are

intercalated between the secondary pinnae, spaced at intervals of 1.5–2.0 cm. (In the middle of the specimen is a detached pinna of *Neuropteris semireticulata* Josten, unconnected with the *N. heterophylla* frond fragment.) If this was

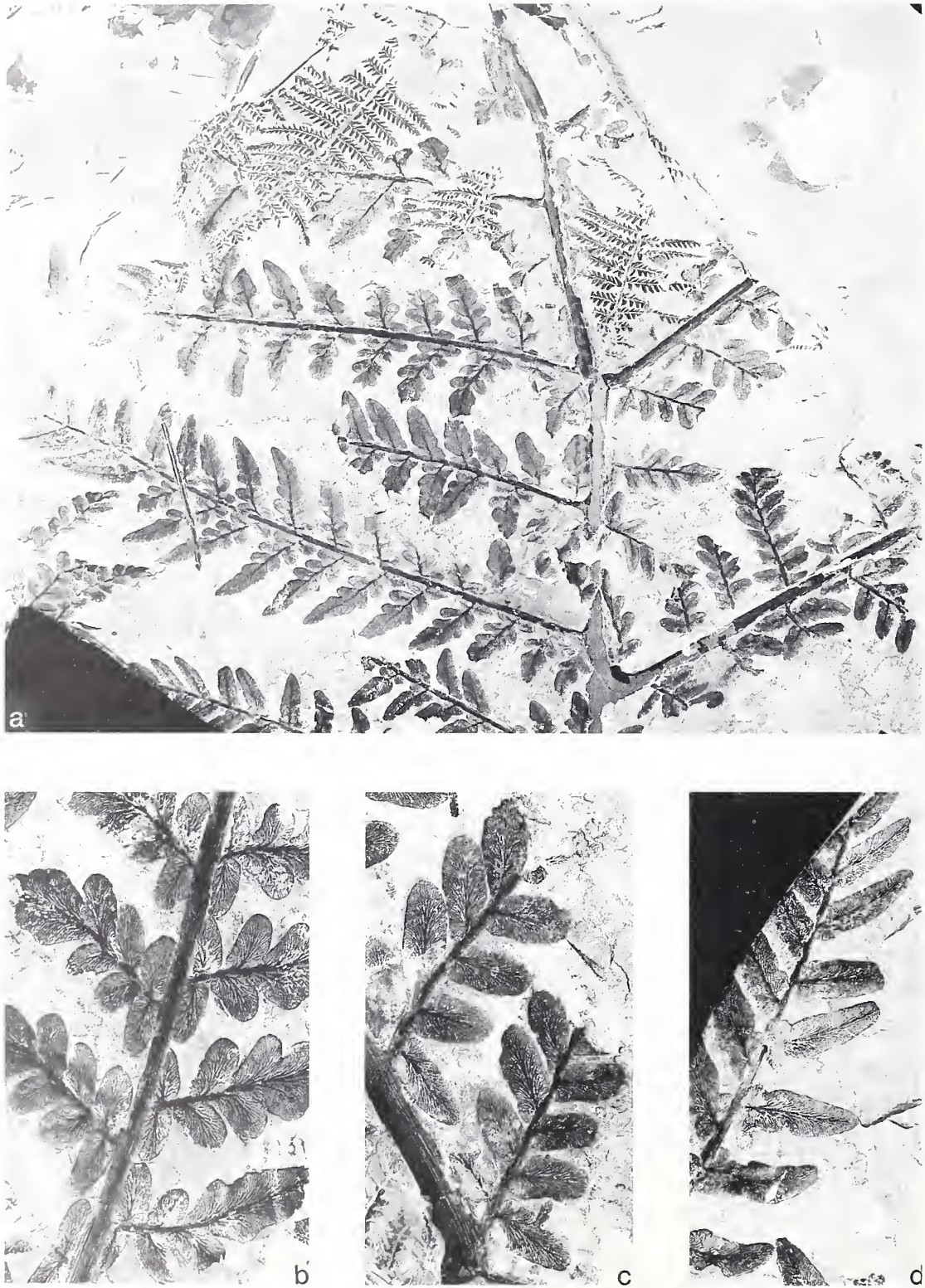


Fig. 2 *Neuropteris heterophylla*, photographed with crossed-polar filters. Fig. 2a, primary rachis immediately above the dichotomy near base of frond. (The pinna fragment shown at the top is of the fern *Senftenbergia plumosa* (Artis) Zeiller.) V.1872,  $\times \frac{2}{3}$ . Figs 2b–d, details of Fig. 2a showing range of form of lateral pinnules,  $\times 1$ . See also Fig. 27a.

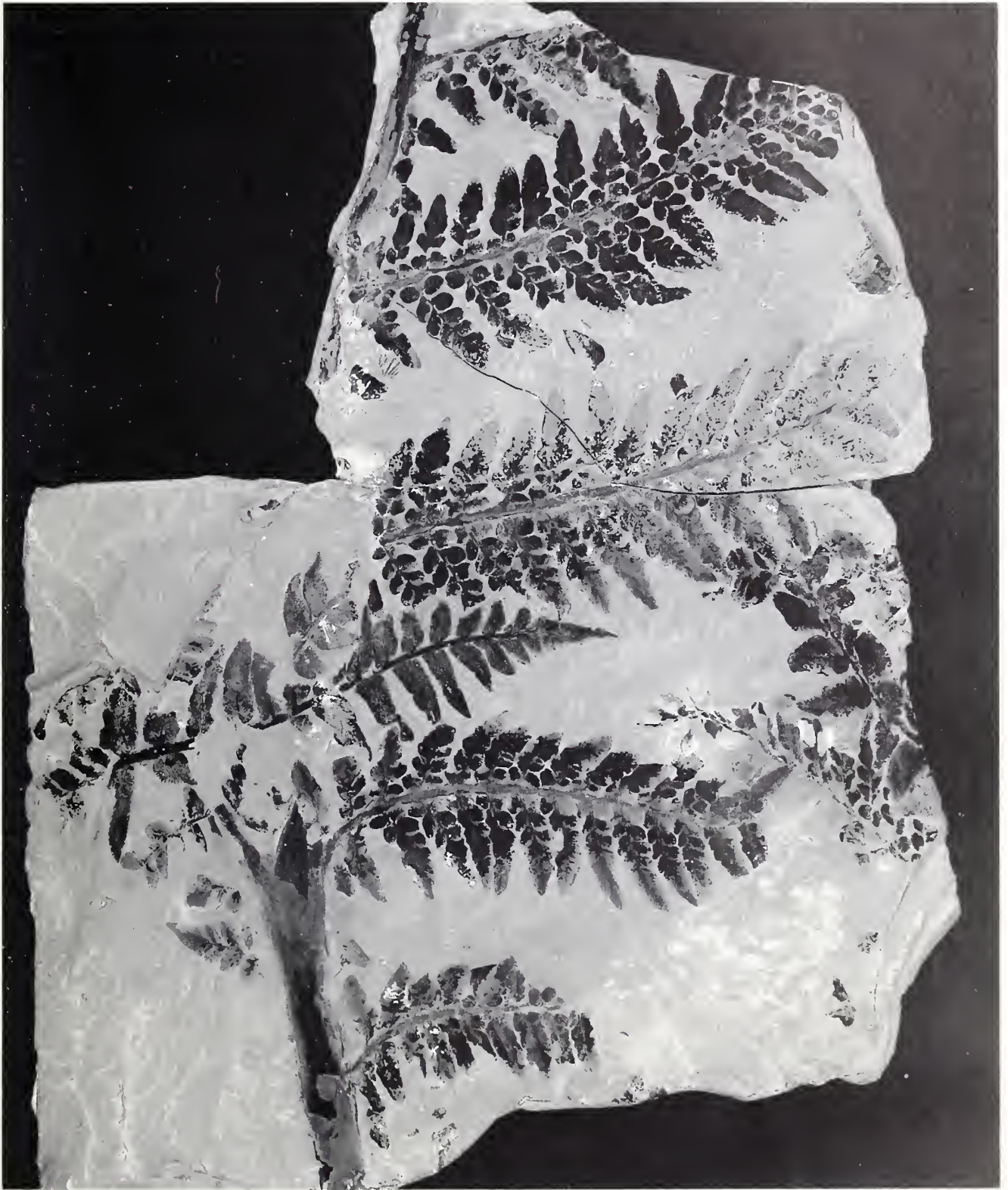


Fig. 3 *Neuropteris heterophylla*. Primary rachis probably just above dichotomy near base of frond, together with a detached fragment of a *N. semireticulata* Josten pinna, photographed with crossed-polar filters. V.63152,  $\times \frac{3}{4}$ . See also Fig. 27b.



Figs 4, 5 *Neuropteris heterophylla*, photographed with crossed-polar filters. Fig. 4, distal part of primary pinna branch. V.1867,  $\times \frac{2}{3}$ . See also Fig. 28c. Fig. 5, two bipinnate pinnae. V.1871,  $\times \frac{2}{3}$ . See also Fig. 28c.

part of a primary rachis from just above the main dichotomy, the greater width of the rachis and spacing of the secondary rachis suggest that it must have originated from a significantly larger frond than the specimens in Figs 1 and 2.

*Distal frond fragments (Figs 4, 6–8, 28).* These are distal segments of tripinnate pinnae, which are markedly asymmetrical about the primary rachis. The secondary pinnae on one side of the primary rachis are both longer and more pinnately divided than on the other. It is probable that the

longer and more divided secondary pinnae were facing outwards from the frond, in which case Figs 4, 6 and 7 show left-hand primary pinna branches, and Fig. 8 a right-hand primary pinna branch. The primary rachis in most of the specimens is more or less straight, except that in Fig. 8, where curvature is accompanied by apparent distortion of the secondary pinnae, and may thus be a taphonomic effect. The widest primary rachis in these distal primary pinna fragments are 6 mm wide (Figs 6–7), and thus overlap with the width of the most distal preserved part of the primary pinnae in Fig. 1.



Fig. 6 *Neuropteris heterophylla*. Near distal part of primary pinna, photographed with crossed-polar filters. V.1868,  $\times \frac{3}{5}$ . See also Fig. 28b.

Secondary pinnae are attached at  $60^{\circ}$ – $90^{\circ}$  (most usually *c.*  $70^{\circ}$ ) on either side of the primary rachis. They are parallel-sided for much of their length, but are gently tapered in their distal part and terminated by a small, rhomboidal apical pinnule, *c.* 1 cm long. The secondary racheis are 0.5–3 mm wide. In the distal part of the frond the secondary pinnae are monopinnate and oppositely arranged at intervals of 1–3 cm; lower in the frond they become bipinnate and alternately arranged at intervals of up to 5 cm. Where the secondary

pinnae are bipinnate, one or two short, monopinnate pinnae are intercalated on the primary rachis between them. They are up to 2 cm long with a rhomboidal apical pinnule, and are spaced at intervals of *c.* 1 cm.

Tertiary pinnae are attached to the secondary racheis at  $80^{\circ}$ – $90^{\circ}$ , except near the secondary pinna apex where they are more oblique (*c.*  $60^{\circ}$ ). They are spaced at intervals of 0.4 cm for the shorter pinnae, increasing to 0.8 cm in the longest preserved pinnae, and are oppositely or sub-oppositely



Fig. 7 *Neuropteris heterophylla*. Distal part of primary pinna, photographed with crossed-polar filters. V.2727,  $\times \frac{2}{3}$ . See also Fig. 28a.

arranged. They are parallel-sided for most of their length, and terminated by a single, rhomboidal apical pinnule, c. 1 cm long.

#### Pinnule morphology

Typical pinnules are shown in Figs 2b–d. They vary from 3 to 15 mm long and are 3–6 mm wide. The smallest pinnules are

round to oval, about as broad as long; but the larger ones are more elongate, parallel-sided to linguaeform with a round apex. The longest pinnules are sometimes subtriangular with a bluntly acuminate apex. An acroscopic and sometimes a basiscopic swelling occurs near the base of the larger pinnules. In the largest pinnules the former becomes more prominent, until it eventually develops into a discrete, subsidiary order pinnule. Except near the pinna apex, the





Fig. 8 *Neuropteris heterophylla*. Distal part of primary pinna, photographed with crossed-polar filters. V.63153,  $\times \frac{2}{3}$ . See also Fig. 28d.

pinnules are at least partially constricted at the base. The degree of constriction is often more pronounced on the aroscopic side, with the pinnule being partially fused to the rachis on the basiscopic side. Only the largest pinnules tend to be equally constricted on both aroscopic and basiscopic sides. The angle of attachment of the pinnules to the rachis is usually  $70^{\circ}$ – $80^{\circ}$ . High in the pinna it sometimes appears to

be as low as  $60^{\circ}$ , but this may be due to taphonomic distortion.

In the smallest pinnules there is little or no evidence of a midvein. In most pinnules, however, a thin midvein arises from the rachis at a low angle on the basiscopic side of the pinnule. It then curves and lies along the long axis of the pinnule. In most pinnules, the midvein is restricted to the

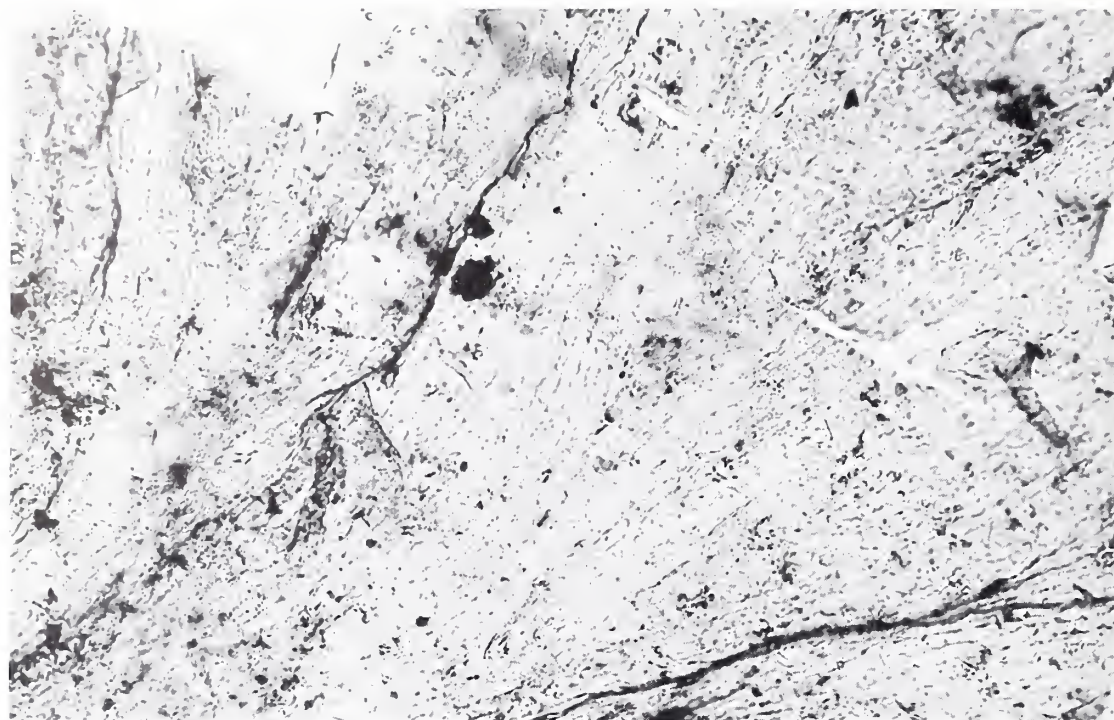


Fig. 9 *Neuropteris heterophylla*. Cuticle from adaxial surface of pinnule showing differentiation of cells in costal and intercostal fields, photographed using bright field illumination. V.2727\$1,  $\times 125$ .

lower half of the pinnule, but in the largest forms it may extend for up to two-thirds of the pinnule length. This decurrent midvein is never very pronounced, being only slightly wider than the lateral veins.

Lateral veins occur alternately on either side of the midvein, attached at intervals of 0.5–1.0 mm. They initially lie at a low angle to the midvein, extend for a short distance in an approximately straight line, and then arch to meet the pinnule margin at  $80^{\circ}$ – $90^{\circ}$ . They may branch up to four times, depending on the width of the pinnule. The angle of branching is usually  $20^{\circ}$ – $30^{\circ}$ , which often gives the veining a somewhat flexuous appearance. The vein density along the pinnule margin may vary from 40 to 55 per cm, but is usually between 48 and 52 per cm.

## Cuticles

The adaxial cuticles from the pinnules appear robust, but have weakly developed intercellular flanges (Fig. 9). There is some differentiation in cell structure in the costal and intercostal fields. In the costal fields, the cells are elongate and subrhomboidal, up to  $150\ \mu\text{m}$  long  $\times$   $20\ \mu\text{m}$  wide (Fig. 17). Their long axes are aligned approximately parallel to the veins. In the intercostal fields the intercellular flanges are very weak, but there is a faint impression of shorter and more irregularly polygonal cells, up to  $50\ \mu\text{m}$  long  $\times$   $20\ \mu\text{m}$  wide (Fig. 18). Again, their long axes are aligned more or less parallel to the veins.

The abaxial cuticles are significantly thinner, and only small fragments could be prepared. Intercellular flanges, although not prominently developed, are clearly visible. Costal cells are elongate, parallel-sided and approximately  $15\ \mu\text{m}$  wide. It was impossible to determine their length. The intercostal cells are irregularly polygonal,  $40$ – $60\ \mu\text{m}$  long and  $12$ – $18\ \mu\text{m}$  wide,

with their long axes aligned parallel to the nervation (Figs 10 and 20).

Stomata are restricted to the intercostal fields of the abaxial surface (Figs 10–11 and 19–22). They are anomocytic, with their polar axes approximately parallel to the veins. Their guard cells are  $20$ – $25\ \mu\text{m}$  long and  $5\ \mu\text{m}$  wide. They do not seem to be significantly sunken.

Papillae occur in the costal fields of the abaxial epidermis (Fig. 10). They are  $30$ – $40\ \mu\text{m}$  wide at their base and  $25$ – $35\ \mu\text{m}$  high. Smaller papillae,  $15$ – $25\ \mu\text{m}$  wide at their base and  $10$ – $20\ \mu\text{m}$  high, also occur in the intercostal fields of the abaxial epidermis (Figs 19–20). They are less densely distributed than in the costal fields, and are mainly on the stomatal neighbour cells, where they appear to over-arch the guard cells (Figs 10–11 and 21–22).

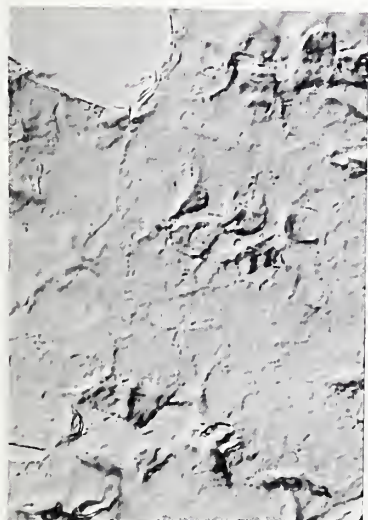
Multicellular trichomes are also restricted to the abaxial epidermis, occurring mainly in the intercostal fields (Figs 12–14 and 23). They are  $25$ – $30\ \mu\text{m}$  in diameter at their base, tapering to  $20\ \mu\text{m}$ . They consist of a uniseriate string of cells  $25$ – $35\ \mu\text{m}$  long, and there is a slight constriction of the trichome at the junction of each cell (Fig. 12). The longest preserved fragment is  $130\ \mu\text{m}$  long, but is clearly incomplete (Fig. 12). Other examples are only  $100\ \mu\text{m}$  long, but seem to be entire and terminated by a swollen cell  $35\ \mu\text{m}$  in diameter, resembling a glandular structure (Figs 13–14). When viewed by SEM, these terminal structures appear to have ruptured, and situated on and near the apex of the trichome is an amorphous mass (Fig. 23; see also Fig. 13 for a view using light microscopy). Similar amorphous masses observed on these cuticles using light microscopy could be seen to have taken the safranin dye, and are almost certainly organic in origin. Being consistently associated with the trichome apices, they are, in our view, probably the remains of exudate produced by the trichomes. However, the volume of this



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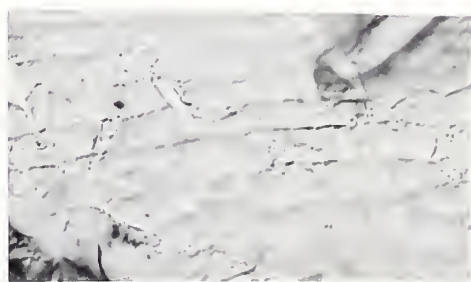
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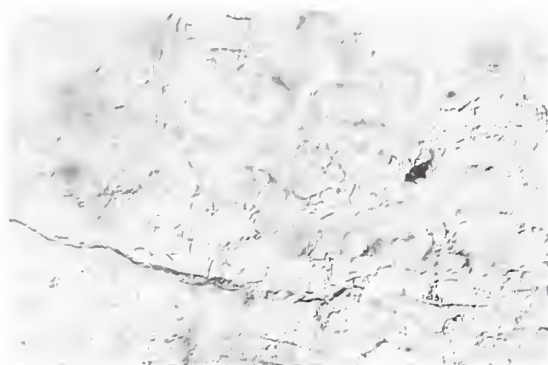


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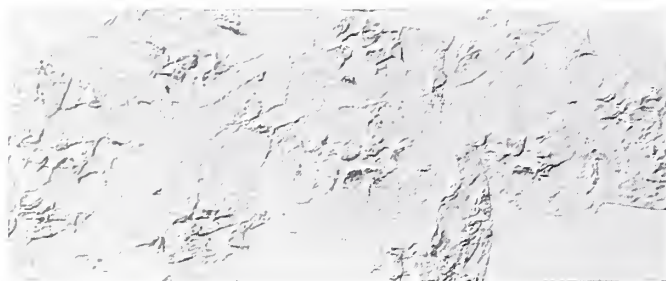
**Figs 10–16** *Neuropteris heterophylla*. Cuticles photographed using Normarski contrast (except Fig. 15). Figs 10–11, cuticles from abaxial surface of pinnule, showing papillate stomata,  $\times 500$ . Fig. 10, V.1867\$2. Fig. 11, V.1867\$1. Figs 12–14, multicellular trichomes from abaxial surface of pinnule,  $\times 500$ . Figs 12–13, V.63152\$2. Fig. 14, V.2727\$8. Fig. 15, cuticle from rachis, using bright field illumination. V.2727\$8,  $\times 125$ . Fig. 16, cuticle from rachis. V.2727\$9,  $\times 500$ .



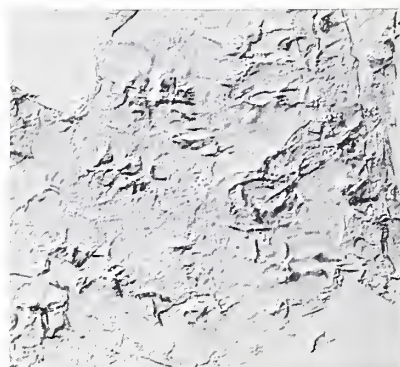
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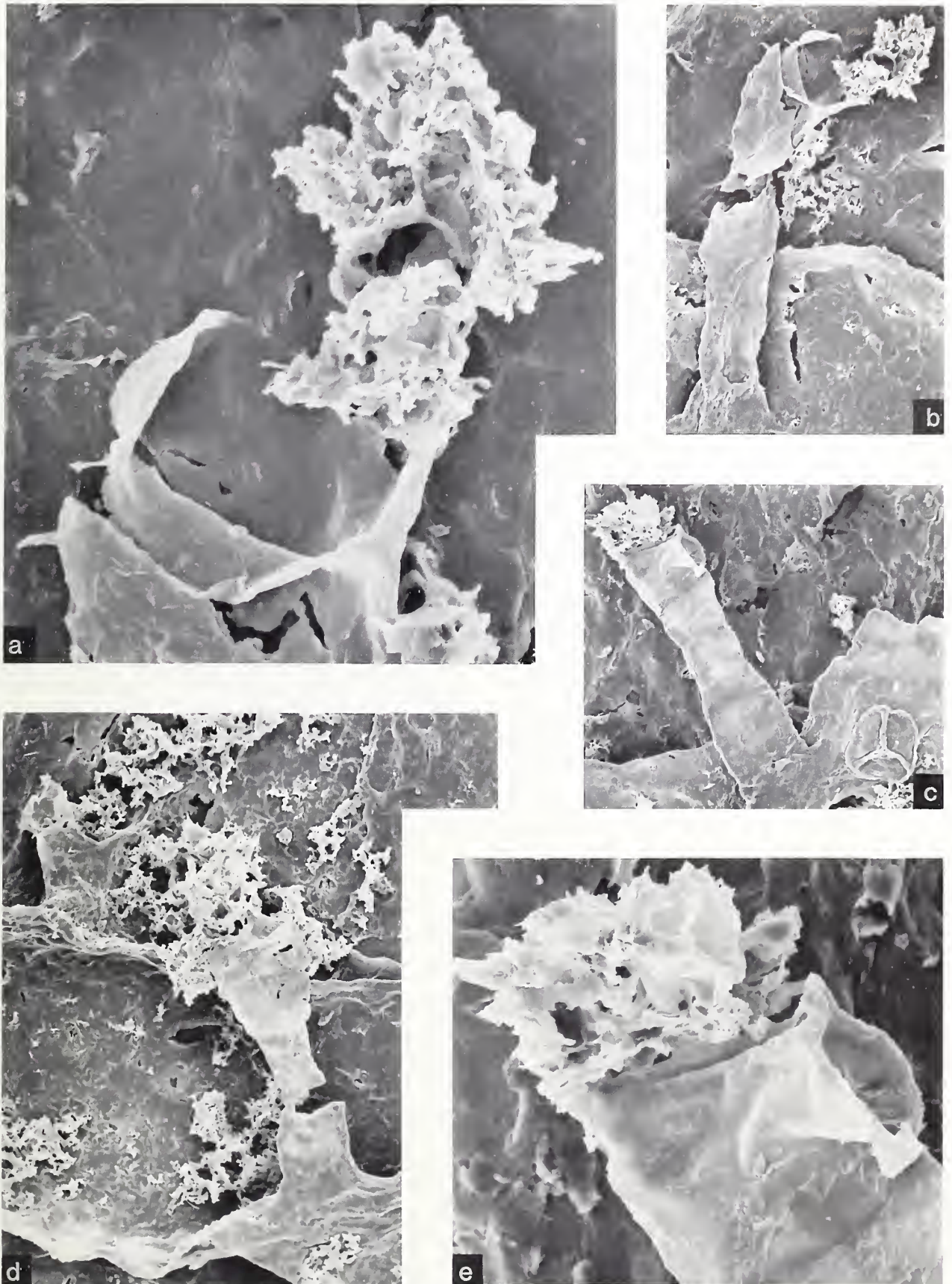
Figs 17–22 *Neuropteris heterophylla*. Cuticles photographed using Normarski contrast. Fig. 17, cuticle from costal field on adaxial surface of pinnule. V.2727\$1,  $\times 250$ . Fig. 18, cuticle from intercostal field on adaxial surface of pinnule. V.1867\$1,  $\times 250$ . Figs 19–20, cuticles from abaxial surface of pinnule, showing parallel alignment of stomatal polar axes. V.1867\$1,  $\times 250$ . Figs. 21–22, details of papillate stomata. V.1867\$1,  $\times 500$ .

exudate often seems larger than could be contained in just the apical cell (e.g. Fig. 23d). This suggests that either the entire trichome functioned as a gland, in which case the transverse cell walls must have broken down when the trichome had become fully developed; or the exudate originated from a superficial cell within the body of the pinnule, and was channelled through the trichome to its apex.

#### Associated miospores

Attached to many of the cuticles prepared during this study were numerous miospores, mostly *c.* 25  $\mu\text{m}$  in diameter (Figs

24–25). Dr B. Owens has kindly examined SEM photographs of some of them and concluded that they are a mixed assemblage, dominated by ?*Lycospora*, ?*Densosporites* and ?*Granulatisporites*. These trilete form-genera are believed to have been mostly produced by lycophytes and ferns (Smith & Butterworth 1967) and are quite different from the monoletic prepollen produced by most medullosans (Stidd 1981). The only possible medullosan male reproductive organ to produce trilete prepollen is *Potonia* (Halle 1933, Florin 1937), which Millay & Taylor (1979) have interpreted as an early offshoot from the main medullosan stock (see also Stidd 1978, 1981). In



**Fig. 23** *Neuropteris heterophylla*. Scanning electron micrographs of multicellular trichomes showing glandular tips with *in situ* exudate. V.2727\$11. Figs 23a and 23e,  $\times 2000$ . Figs 23b–d,  $\times 500$ .

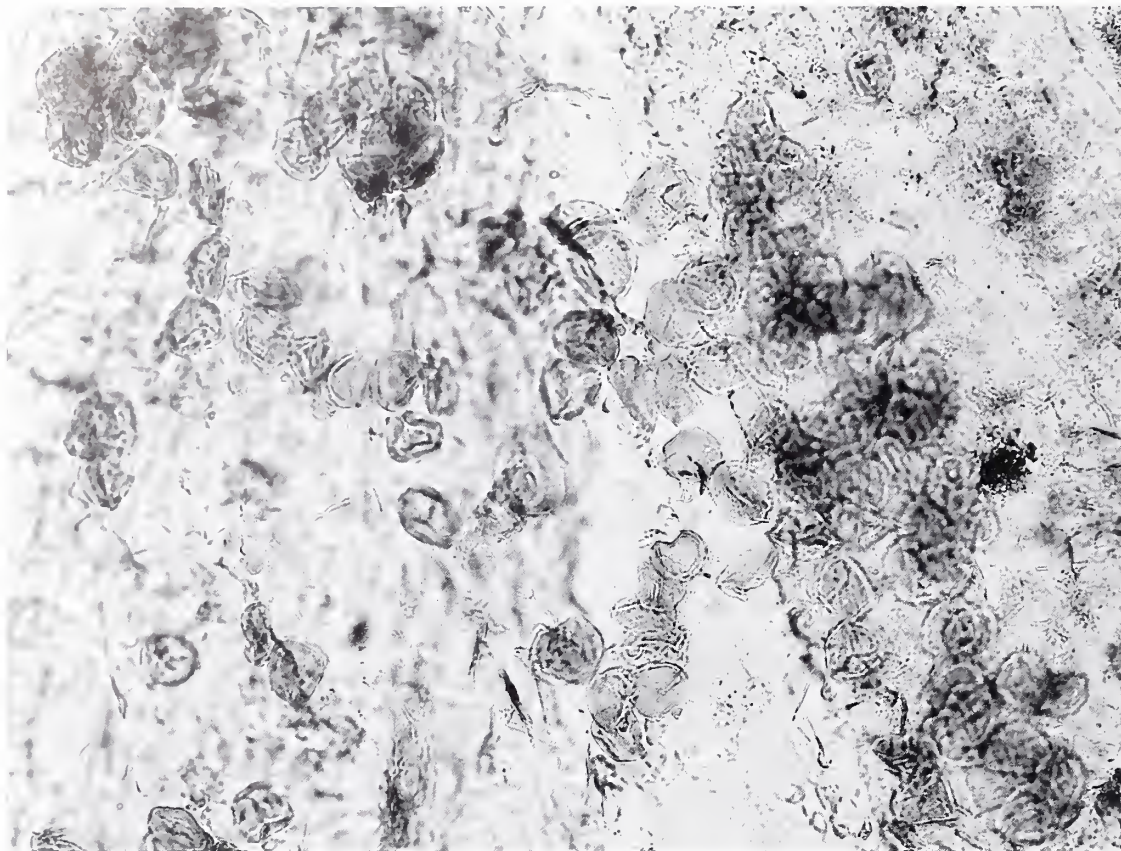


Fig. 24 *Neuropteris heterophylla*. Cuticle from abaxial surface of pinnule, photographed using bright field illumination, showing numerous spores attached. V.2727\$2,  $\times 250$ .

any case *Potonia* prepollen is significantly larger (40–90  $\mu\text{m}$  in diameter), has a less prominent tetrad mark than the miospores attached to our cuticles, and displays a distal sulcus. In our view, therefore, the miospores are unlikely to have anything to do with the plant which produced the *N. heterophylla* fronds. They probably only reflect the general spore/pollen rain in these lycophyte-dominated forests.

## DISCUSSION

### Reconstruction of frond

Based mainly on the specimens from Clay Cross described in this paper, we propose a reconstruction of the *N. heterophylla* frond, shown in Fig. 29. For convenience, the specimens have been reproduced at a unified scale as drawings (Figs 26–28), and the following discussion will refer to these rather than the photographs illustrated earlier in the paper. The reconstructed frond shows the following key features.

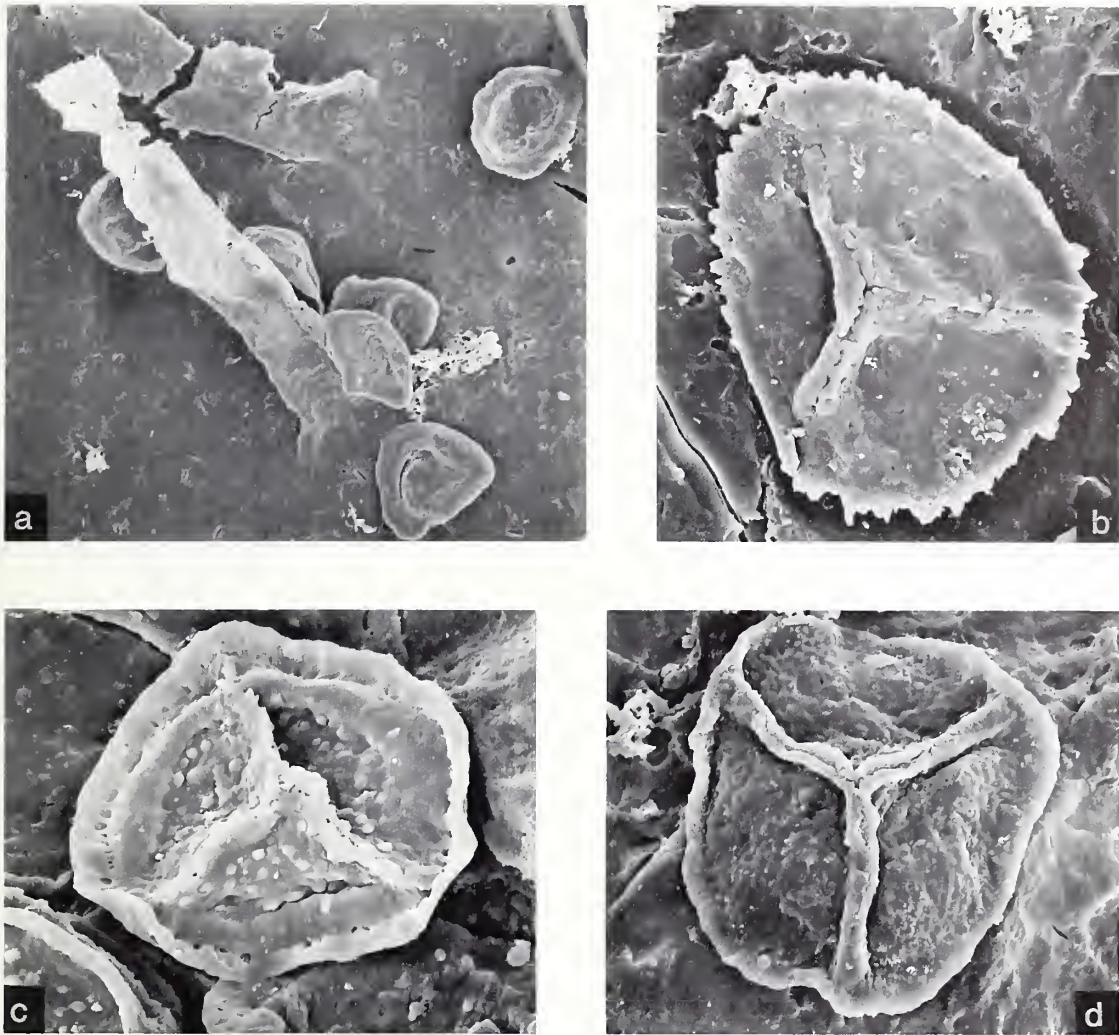
*Dichotomy of primary rachis.* This is particularly well seen in Fig. 26. The dichotomy is wide-angled and the resulting branches curve distally towards one another. It is also shown by the specimen figured by Brongniart (1831: pl. 71). Brongniart's drawing of this specimen suggests that the fork was a lateral branch, but Laveine's (1967: pl. A) photograph clearly shows that the right-hand side of the frond

fragment is distorted. Taking this distortion into account, Brongniart's specimen shows the same pattern of branching as our Fig. 26, and differs only in having a narrower primary rachis and closer-spaced secondary pinnae (see comments below on estimated frond sizes).

Another, but less complete specimen figured by Laveine (1967: pl. M, fig. 1), part of which is also figured by Zeiller (1886: pl. 44), shows part of the frond just above the dichotomy. The two primary pinna branches lie at  $\approx 80^\circ$  to each other, although the dichotomy itself is not preserved.

*Architecture below dichotomy.* The specimen in Fig. 26 shows little of the frond below the dichotomy, but some evidence about this part of the frond is supplied by the specimen figured by Brongniart (1831: pl. 71). A 4-cm length of the main rachis below the dichotomy is preserved, and has monopinnate pinnae attached on either side. The only other specimen which probably shows this part of the frond is that illustrated by Crookall (1959: pl. 33, fig. 2), which has a rachis 0.9 cm wide, bearing short monopinnate pinnae. It compares favourably with the structure and dimensions of that part of the Brongniart (1831) specimen lying below the dichotomy, and it is difficult to see where else it could have occurred in the frond. The Crookall specimen is 13 cm long, and this is thus the minimum distance below the dichotomy that these monopinnate pinnae could have been attached.

There is no evidence of orbiculoid cyclopterid pinnules being attached to the primary rachis near the dichotomy, as in *Laveineopteris loshii* (Brongniart) Cleal *et al.* (von Roehl,



**Fig. 25** *Neuropteris heterophylla*. Scanning electron micrographs of spores attached to cuticle from abaxial surface of pinnule, V.2727\$11. Fig. 25a, cluster of spores near base of multicellular trichome,  $\times 500$ . Fig. 25b, unidentified azonate spore with equatorial ornamentation. Fig. 25c, ?*Densosporites* sp. Fig. 25d, ?*Granulatisporites* sp. Figs 25b–d,  $\times 2000$ .

1868: pl. 17), *Laveineopteris rarineris* (Bunbury) Cleal *et al.* (Carpentier, 1930: pl. 8; Gothan, 1953: text-fig. 8; Laveine, 1967: pl. 41, fig. 3; pl. 45, fig. 3; pl. O, fig. 1). The specimen identified as *N. heterophylla* with possible cyclopterids attached (Gothan, 1953: text-fig. 6) has been re-identified as *L. loshii* by Laveine (1967). The architecture seen in *N. heterophylla* is nearer to that of *N. obliqua* (Gothan, 1953: text-fig. 7) and *N. ovata* Hoffmann (Zodrow & Cleal 1988). Neither V.1797 nor the specimen figured by Brongniart (1831: pl. 71) show any evidence of the type of enlarged pinnules present in the lower part of the *N. ovata* and *N. obliqua* fronds (sometimes referred to as forma *impar* pinnules). However, the specimen of *N. heterophylla* illustrated by Laveine (1967: pls 11–12), which is probably part of a left-hand primary pinna just above the basal dichotomy, seems to have large, subtriangular pinnules, similar in shape to the forma *impar* pinnules from the base of the *N. obliqua* fronds.

**Primary pinna branches immediately above dichotomy.** A distinctive feature of *N. heterophylla* is the way that the primary pinna branches compensate for the reduced space

available on their inward-facing side, due to the curvature of the primary rachis. It is achieved by the secondary pinnae being alternately long and short along that part of the primary rachis showing maximum curvature. It has not been demonstrated in any other neuropteroid species, nor in related fronds such as *Odontopteris* (Zeiller 1906) or *Callipteridium* (Wendel 1980). It can be clearly seen in Figs 26 and 27a.

**Primary pinna terminals.** These are well shown in Figs 28a–d. Another example was figured by Zeiller (1879: pl. 164, fig. 1; refigured by Zeiller, 1886: pl. 43, fig. 1). They become tripinnate at only a short distance from the pinna apex, and are normally distinctly asymmetrical about the primary rachis. This asymmetry is almost certainly a continuation of the asymmetry of the lower part of the primary pinna, with the side with the longer secondary pinnae facing outwards from the frond.

The small specimen shown in Fig. 28e may also have come from near a primary pinna terminal. However, bipinnate pinnae are also known attached to the inward-facing side of the primary pinna, lower in the frond (e.g. c. 40 cm above the dichotomy in Fig. 26). Since only two pinnae are shown in

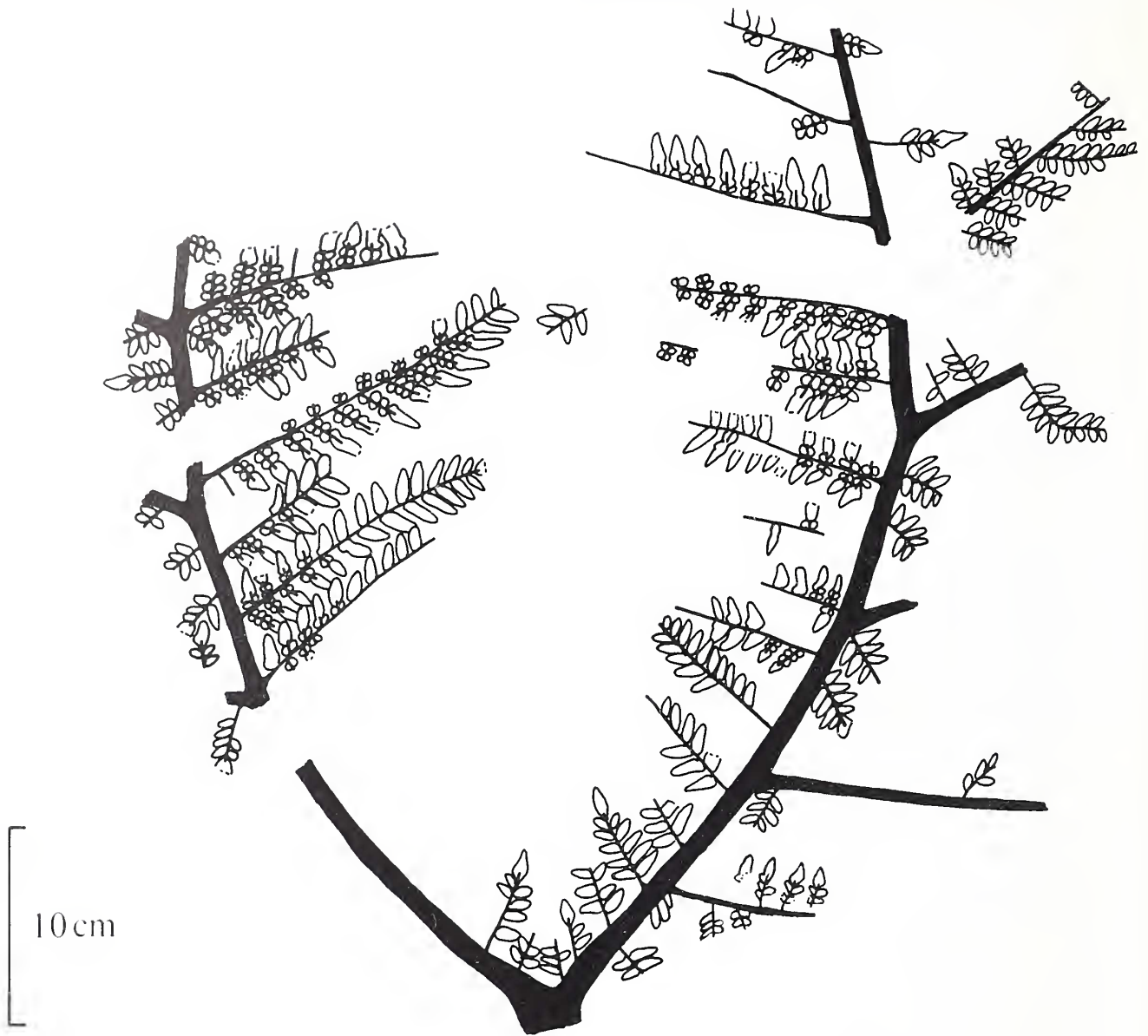


Fig. 26 *Neuropteris heterophylla*. Drawing of specimen shown in Fig. 1, showing dichotomy of primary rachis near the base of the frond. V.1797,  $\times 0.3$ .

Fig. 28e, it is impossible to determine whether they are alternating long and short, as is characteristic of the lower part of the frond. This demonstrates the difficulty of positioning such small specimens within so complex a structure as the *N. heterophylla* frond.

*Size and degree of pinnation of secondary pinnae.* No complete secondary pinnae have been found attached to the outward-facing sides of the primary pinnae in the basal part of the frond. The longest known examples are 13 cm long (Fig. 26; see also Laveine, 1967: pl. 11, fig. 1), but are clearly very incomplete. The longest detached example is probably that shown in Crookall (1959: pl. 25, figs 1–2). It is a 17-cm long near terminal fragment of a bipinnate pinna. It is more or less symmetrical about the penultimate rachis, and is thus quite different from the asymmetrical terminals of the primary pinnae (discussed above). In nearly all of the known speci-

mens, these outward-facing secondary pinnae are bipinnate. Just one (Laveine, 1967: pls 11–12) shows a tendency to become tripinnate.

*Size of frond.* None of the specimens described in this study, or documented in the literature, are complete enough to give a very reliable estimate of the overall size of the frond. However, using the largest available specimen (Fig. 26) it is possible to assess the approximate distance from the dichotomy to the frond apex (hereafter referred to as the DAD). Assuming that the two primary pinna branches, which curve distally in towards one another, did not overlap significantly at the frond apex, then the DAD in this frond was about 1 m. Using this as a base-line, it is possible to estimate the DAD of fronds in other, less complete specimens, using the assumption that frond size is broadly correlated with primary rachis width (PRW) and the spacing



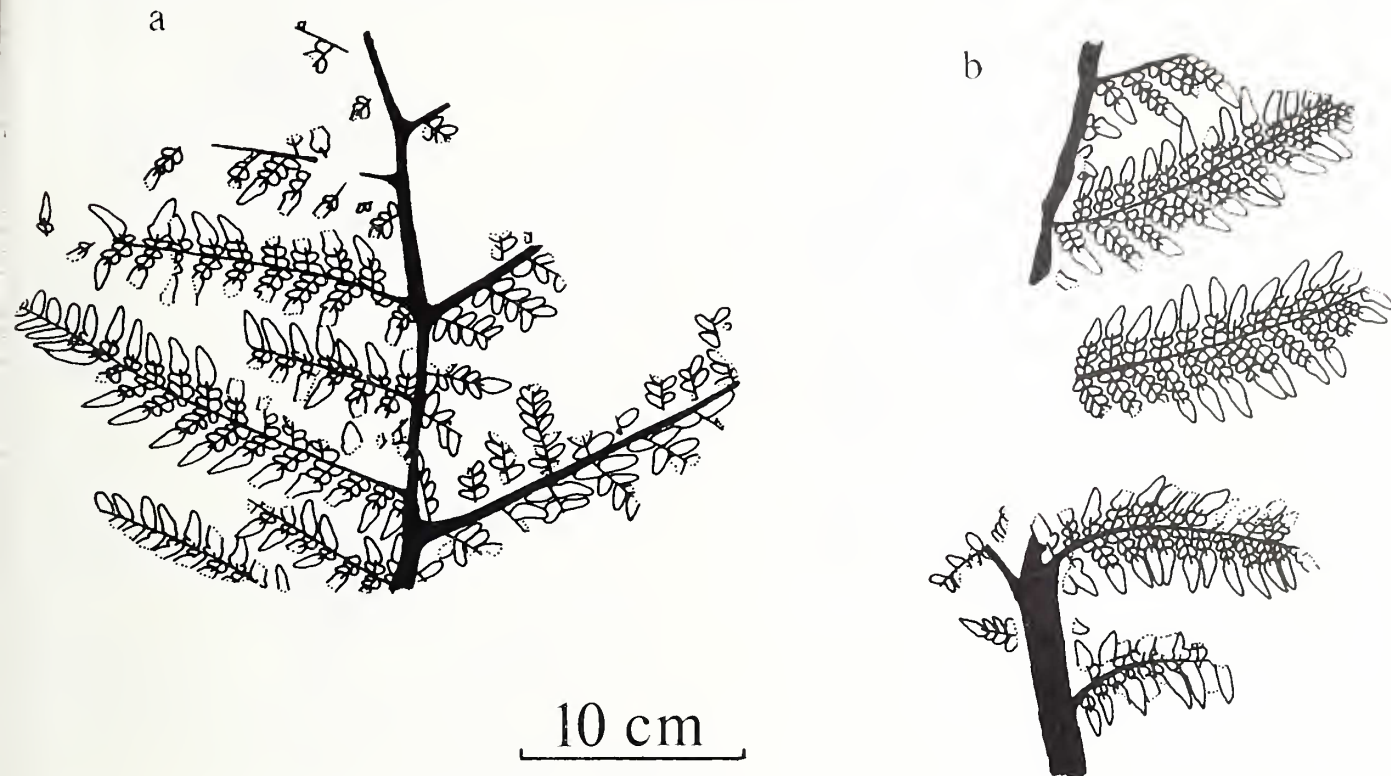


Fig. 27 *Neuropteris heterophylla*. Drawings of specimens shown in Figs 2–3, showing parts of primary rachis near the main dichotomy of the frond. Fig. 27a, V.1872. Fig. 27b, V.63152. Both  $\times 0.3$ .

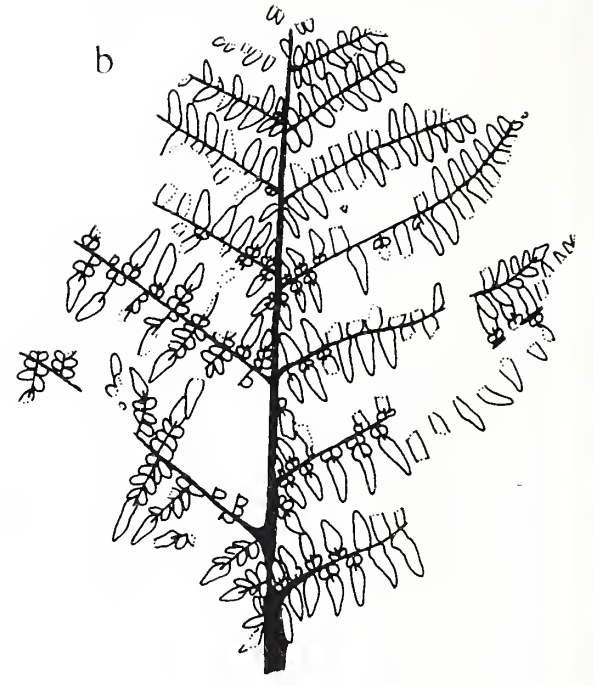
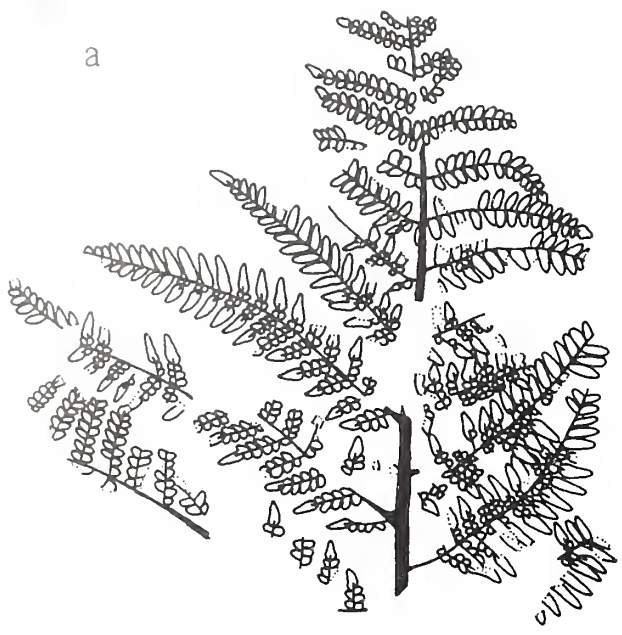
between secondary racheis (SRS) in comparable parts of the frond.

- a. The smaller fragment shown in Fig. 27a has PRW and SRS dimensions comparable to a position about 35 cm above the dichotomy in Fig. 26. Consequently, it is also probably from a frond with a DAD of c. 1 m.
- b. The specimen figured by Zeiller (1886: pl. 44) and Laveine (1967: pl. M, fig. 1) also has PRW and SAS dimensions similar to that in our Fig. 26. Its DAD is therefore again estimated to be c. 1 m.
- c. The specimen figured by Brongniart (1831: pl. 71) has a PRW immediately below the dichotomy of 1.4 cm, and a SAS on the outward-facing side of the frond just above the dichotomy of 4–5 cm. These dimensions are about half those in Fig. 26, and so the DAD is estimated as c. 0.5 m.
- d. Fig. 27b shows a curved primary rachis with a PRW 1.5–1.0 cm and a SAS of c. 6 cm. If this was the proximal part of a primary pinna branch, then the PRW is approximately twice that in Fig. 26, and consequently the DAD would be c. 2 m. It is true that Fig. 27b does not show the alternating long and short secondary pinnae normally characterizing the proximal part of the frond, but this may simply be because the secondary pinnae were more widely spaced, reducing the competition for space in this part of the frond. The only alternative position for such a specimen would be below the dichotomy, but the marked tapering of the primary rachis, and the presence of bipinnate secondary pinnae (only monopinnate secondaries have been otherwise found in this part of the frond) tend to argue against this.

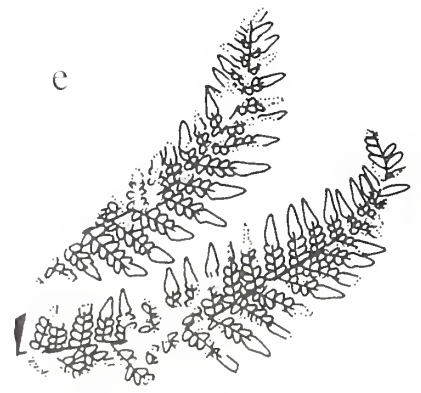
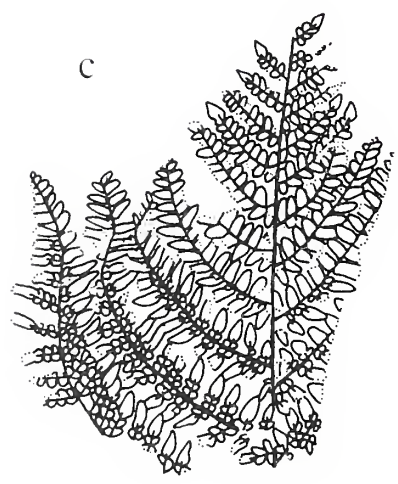
From the above evidence, it appears that the DAD of the fronds was normally 0.5–1.0 metres, possibly sometimes reaching 2.0 metres. To translate this into an estimate of the total length of the foliage-bearing part of the frond, it would be necessary to know how far the foliage extended below the dichotomy. There is little unequivocal evidence on this. The specimen figured by Brongniart (1831: pl. 71) shows 4 cm of frond below the dichotomy. However, if the specimen figured by Crookall (1959: pl. 33, fig. 2) has been correctly interpreted as part of a primary rachis below the dichotomy (see p. 166), then there was at least 13 cm of foliage below the dichotomy in a small frond. This suggests that there may have been at least 30 cm of foliage below the dichotomy in one of the fronds with a DAD of 1 metre, and perhaps 60 cm or more in the largest fronds. Combining this evidence, we suggest that the overall length of the foliage-bearing part of the frond may have varied from 0.7 m to 2.6 m, the most commonly found probably being about 1.3 m long. There is no evidence available as to the length of the petioles, and so it is impossible to estimate the complete length of the frond, from its point of attachment to the stem to the apex.

No complete outward-facing secondary pinnae are preserved, so the width of the frond cannot be determined. Fig. 26 shows a width of 0.6 m, but the secondary pinnae are clearly very incomplete, and the total frond width may have been 1.0 m or more. If this estimate is correct, then that part of the frond lying above the primary pinna dichotomy must have been as wide as it was long.

*General comments on frond architecture.* The type of bipartite frond reconstructed in Fig. 29 broadly reflects the



10 cm



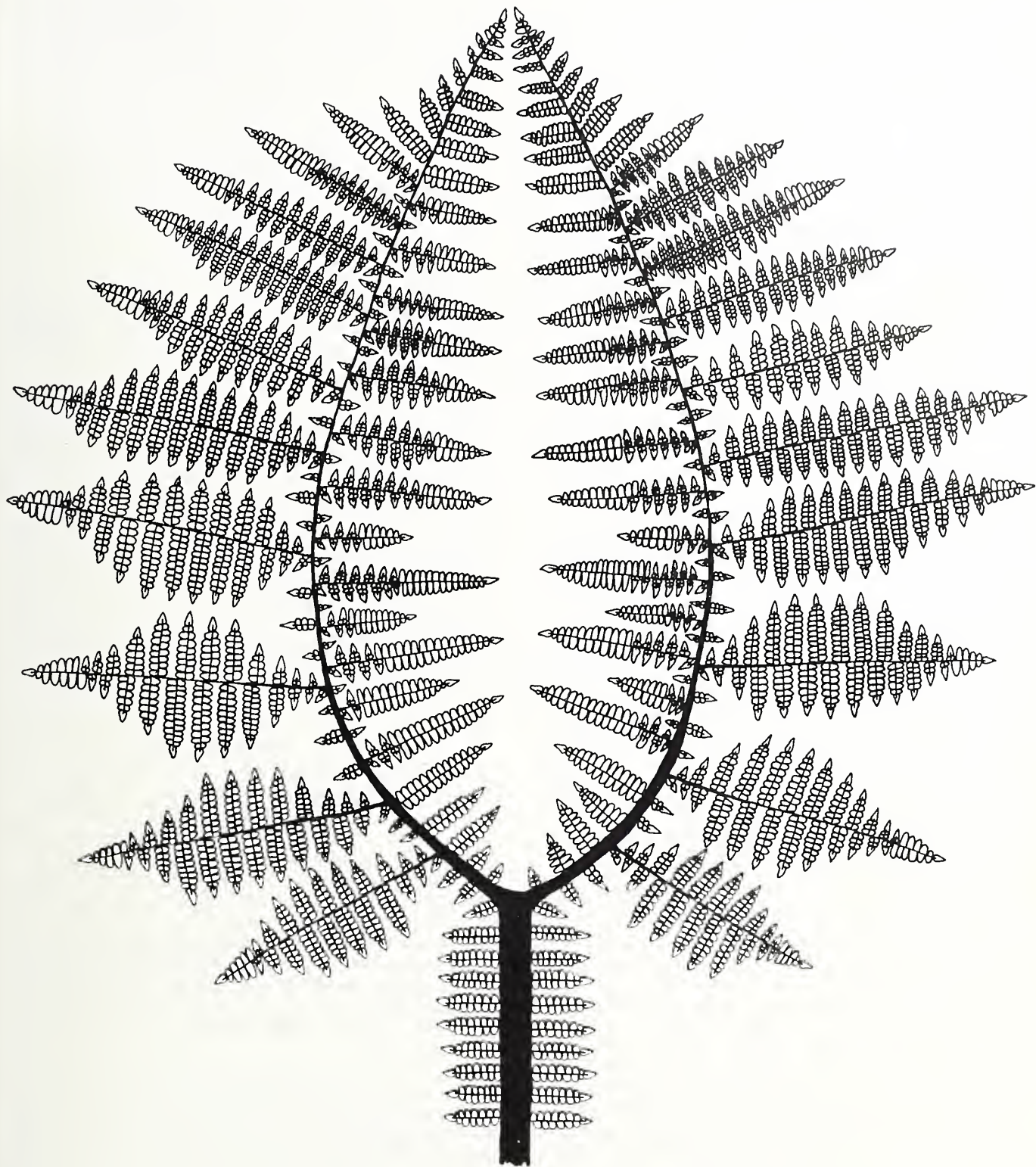


Fig. 29 *Neuropteris heterophylla*. Proposed reconstruction of average-sized frond. About one seventh natural size.

Fig. 28 *Neuropteris heterophylla*. Drawings of specimens shown in Figs 4–8, showing near terminal parts of primary pinnae. Fig. 28a, V.2727. Fig. 28b, V.1868. Fig. 28c, V.1867. Fig. 28d, V.63153. Fig. 28e, V.1871. All  $\times 0.3$ .

structure envisaged by Gothan (1941) for *Neuropteris* (syn. *Imparipteris*), except for the absence of orbicular cyclopterid pinnules at the base. Although varying in detail, such a bipartite structure is extremely common in Palaeozoic pteridosperm fronds, occurring in the Calamopityales, Callistophytales and Lyginopteridales, as well as the Trigonocarpales (Daber 1980, Gastaldo 1988); only the Peltaspermales fronds are normally characterized by exclusively pinnate branching (Kerp 1986). It thus occurs in both classes of Palaeozoic pteridosperms (the Ginkgoopsida and Cycadopsida *sensu* Meyen, 1987), which are believed to have evolved independently from the progymnosperms. Consequently, the bipartite frond structure also probably developed independently in the two classes. Its function is at present unclear, but may have maximized the width of each frond without developing excessively long rachis, particularly those of the second order. For structural reasons, the longer a rachis becomes, the wider it must be, particularly in its proximal part. Since the rachis probably had no photosynthetic function (they show no evidence of stomata), minimizing the rachis:lamina bulk ratio would help increase the efficiency of the frond as a whole.

### Significance of epidermal structures

Based mainly on cuticle evidence, Cleal & Zodrow (1989) divided *Neuropteris* into four main groups. Elucidating the epidermal structure of *N. heterophylla* has had important consequences for the nomenclature of this group of foliage, since it has allowed the four groups to be made the basis of a formal taxonomy. Full details of the revised nomenclature are presented by Cleal *et al.* (1990), but the results may be summarized as follows.

Group 1 = *Laveineopteris* Cleal, Shute & Zodrow 1990

Group 2 = *Neuropteris* (Brongniart) Sternberg *emend.* Cleal, Shute & Zodrow 1990

Group 3 = *Macroneuropteris* Cleal, Shute & Zodrow 1990

Group 4 = *Neurocallipteris* Sterzel *emend.* Cleal, Shute & Zodrow 1990

From the preconceptions of earlier authors (e.g. Bertrand, 1930) *N. heterophylla* might be expected to fall into Group 1 of this classification (i.e. with '*N.*' *loshii*, '*N.*' *tenuifolia* and '*N.*' *rarinervis*). However, the epidermal characters found in the present study place it clearly in Group 2 (i.e. with *N. ovata* and *N. flexuosa*). These are: the cell structure in the costal and intercostal fields are clearly differentiated on the adaxial surface; the stomata are anomocytic; cell structure is clearly visible on the abaxial cuticle; and there are both papillae and multicellular trichomes on the abaxial cuticle.

Although multicellular trichomes are present in other neuropteroid species (Barthel 1961, 1962, Cleal & Zodrow 1989), this is the only one reported to have glandular-tipped hairs. In some of the specimens, what appear to be the remains of the exudate produced by the glands are preserved. To the best of our knowledge, this is the oldest evidence of *in situ* exudate preserved in the fossil record. It seems to have been a sticky, resinous substance, which also covered at least part of the abaxial surface of the frond, causing numerous miospores to adhere to it. Whether this condition was the result of taphonomic breakdown of the glandular tips, causing the exudate to become spread over the frond surface, or whether the exudate covered the frond surface in life, is not clear. Its function is also not certain, although a protective role against herbivorous insect attack would seem possible. It

has been noted elsewhere that there is little direct evidence of insect attack in medullosan foliage and that they must have had some defence against it (Cleal & Laveine 1988, Cleal & Zodrow 1989). The sticky exudate produced by the hairs of *N. heterophylla* could well have been a deterrent to such attack, although it seems strange that this is the only neuropterid known to adopt such a strategy. On the other hand, Beerbower *et al.* (1987) argued that herbivory was not a significant feeding mode for Carboniferous arthropods, in which case the exudate may have had an alternative, perhaps excretory function.

### Taxonomy

Laveine (1967) has reported that the type specimen of *N. heterophylla* figured by Brongniart (1822) is lost. He therefore nominated a specimen figured by Brongniart (1831: pl. 71) as neotype, and illustrated a photograph of it.

In the absence of direct evidence of reproductive organs or stem/rachis anatomy, the taxonomic position of *N. heterophylla* can only be determined from circumstantial evidence. We have provisionally placed it in the pteridosperm order Trigonocarpales Meyen based on its similarity, in both frond architecture and epidermal structure, to *Neuropteris ovata*, which Beeler (1983) has reported attached to *Medullosa noei* Steidtmann stems. As with most species of trigonocarpalean foliage, the identification of *N. heterophylla* has traditionally depended on the shape and nervation of the pinnules, and we have been able to add little to the description of these features given by Laveine (1967). We have, however, been able to add details of its epidermal structure, which require the diagnosis to be enlarged. The taxonomy may be summarized as follows.

Division PINOPHYTA Meyen, 1987

Order TRIGONOCARPALES Meyen, 1987

Form-genus **NEUROPTERIS** (Brongniart) Sternberg *emend.* Cleal *et al.* 1990

#### *Neuropteris heterophylla* (Brongniart) Sternberg

1822 *Filicites* (*Neuropteris*) *heterophyllus* Brongniart: 239; pl. 2, fig. 6.

1825 *Neuropteris heterophylla* (Brongniart) Sternberg: xvi.

1967 *Neuropteris heterophylla* (Brongniart) Sternberg; Laveine: 140; pl. A; pl. B, fig. 1; pls 11–13 (q.v. for synonymy).

1990 *Neuropteris heterophylla* (Brongniart) Sternberg; Cleal *et al.*: 487.

DIAGNOSIS. Ultimate pinnae oval and imparipinnate. Pinnules oval, sometimes somewhat triangular, generally with round apex. Pinnule base cordiform in proximal part of pinna; towards pinna apex becoming attached to rachis by up to half of its catadromic side. Apical pinnules usually broad with round apex, and length: breadth ratio 1–2; on short pinnae, more elongate with an obtuse apex. Nervation dense. Midvein visible for about half of the pinnule length and rather strong at base. Thick, somewhat flexuous lateral veins arise from midvein at acute angles, dichotomize two to four times, and reach pinnule margin at oblique angles. Adaxial cuticle thicker than abaxial. Adaxial epidermal cells sub-rhomboidal, more elongate in costal fields. Papillae and

glandular multi-cellular trichomes abundant on abaxial epidermis. Stomata anomocytic, only on intercostal fields of abaxial epidermis; polar axes more or less parallel to veins.

### Comparison with other species

*Neuropteris heterophylla* is most similar to *N. obliqua* (Brongniart) Zeciler and isolated fragments are easily confused. However, the former has rounder lateral pinnules, attached more narrowly to the rachis; and broader, more deltoid apical pinnules with a rounder apex. Also, it does not have the large subtriangular pinnules (known as forma *impar*) that characterize the basal part of the *N. obliqua* frond. The epidermal features of *N. obliqua* are at present unknown (cuticles identified as this species by Barthel, 1962, in fact belong to *Laveineopteris loshii* (Brongniart) Cleal *et al.* – see Laveine, 1967).

Also very similar is the holotype of *Neuropteris grangeri* Brongniart, which originated from the Pennsylvanian of Ohio, USA (Laveine 1967: pl. H, fig. 2). The American specimen has pinnules with a more obtuse apex than is typical for *N. heterophylla*, and lateral veins that meet the pinnule margin at a less oblique angle. However, not enough material has been described from the type area of *N. grangeri* to determine the range of its morphological variation, and so a full comparison with *N. heterophylla* is impossible.

Many of the European records of *N. grangeri* were transferred to *Neuropteris ghayei* Stockmans & Willièrè by Stockmans & Willièrè (in Pastiels & Willièrè, 1954). *N. ghayei* is very similar to *N. heterophylla*, but has rather larger, rounder, thicker-limbed pinnules. Furthermore, the midvein of *N. ghayei* is only well developed near the base of the pinnule and the lateral veins are more flexuous, sometimes pseudoanastomosed. It also tends to have more tapered ultimate pinnae. The epidermal structure of *N. ghayei* is unknown.

It can be difficult to distinguish the smaller pinnules of *N. heterophylla* and *Laveineopteris loshii* (Brongniart) Cleal *et al.*, which are more or less oval in both species. However, the larger pinnules of the latter are more linguiform and have a more prominent midvein extending for at least  $\frac{2}{3}$  of the pinnule length. Also, *L. loshii* has more broadly arched lateral veins, which meet the pinnule margin at a less oblique angle and are never flexuous. There is also a significant difference in the cuticles. The adaxial epidermal cells of *L. loshii* do not differ significantly between the costal and intercostal fields; the abaxial cuticle shows little evidence of cell structure, other than the stomatal guard cells, and there are neither papillae nor the glandular hairs as found in *N. heterophylla*.

*Laveineopteris tenuifolia* (Sternberg) Cleal *et al.* could be confused with the larger pinnules of *N. heterophylla*, but are generally more linguiform, have a more prominent midvein extending for up to  $\frac{3}{4}$  of the pinnule length, and non-flexuous lateral veins. The epidermal structure of *L. tenuifolia*, which is essentially identical to that of *L. loshii*, also serves to distinguish it from *N. heterophylla* (see previous paragraph).

The specimens described by Wills (1914) as *N. heterophylla* are difficult to assess. Only one figured specimen shows features of the gross morphology, and this is a single, small pinnule, probably from a near-terminal position in a pinna. It shows none of the characters necessary to place it in a particular species. The cuticles figured by Wills are quite different from those of *N. heterophylla*, lacking the promi-

nent papillae on the abaxial surface, and having cyclocytic stomata with a ring of significantly thickened subsidiary cells. Based on the epidermal characters, Wills' specimens are closest to *Macroneuropteris scheuchzeri* (Hoffmann) Cleal *et al.*, but it would be difficult to reconcile such an identification with the small size of the pinnules.

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